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A dynamic model of metabolizable energy utilization in growing and mature cattle. III. Model evaluation

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ABSTRACT: Component models of heat production identified in a proposed system of partitioning ME intake and a dynamic systems model that predicts gain in empty BW in cattle resulting from a known intake of ME were evaluated. Evaluations were done in four main areas: 1) net efficiency of ME utilization for gain, 2) relationship between recovered energy and ME intake, 3) predicting gain in empty BW from recovered energy, and 4) predicting gain in empty BW from ME intake. An analysis of published data showed that the net partial efficiencies of ME utilization for protein and fat gain were approximately 0.2 and 0.75, respectively, and that the net efficiency of ME utilization for gain could be estimated using these net partial efficiencies and the fraction of recovered energy that is contained in protein. Analyses of published sheep and cattle experimental data showed a significant linear relationship between recovered energy and ME intake, with no evidence for a nonlinear relationship. Growth and body composition of Hereford × Angus steers simulated from weaning to slaughter showed that over the finishing period, 20.8% of ME intake was recovered in gain. These results were similar to observed data and comparable to feedlot data of 26.5% for a shorter finishing period with a higher-quality diet. The component model to predict gain in empty BW from recovered energy was evaluated with growth and body composition data of five steer genotypes on two levels of nutrition. Linear regression of observed on predicted values for empty BW resulted in an intercept and slope that were not different ($P < 0.05$) from 0 and 1, respectively. Evaluations of the dynamic systems model to predict gain in empty BW using ME intake as the input showed close agreement between predicted and observed final empty BW for steers that were finished on high-energy diets, and the model accurately predicted growth patterns for Angus, Charolais, and Simmental reproducing females from 10 mo to 7 yr of age.

Key Words: Beef Cattle, Energy Metabolism, Models

Introduction

Computer models of biological systems use mathematical relationships to represent biological processes that are responsible for the conversion of inputs to outputs. Dynamic simulation models have the advantage of accommodating a wider range of management options and transition states that may be difficult to handle with static systems. These dynamic models are input driven and are ideal for studying animal response to changes in nutritional management. For a model to be accepted and used with confidence, it should be demonstrated that it is capable of representing the actual system under a wide range of environmental conditions with a reasonable degree of accuracy. This infor-

mation can only be gained through an extensive evaluation of the model, and this is critical to the success and credibility of any model. Williams and Jenkins (2003a,b) proposed a system to partition ME intake **(MEI)** in cattle, and developed models to estimate components of heat production identified in this ME partitioning system. These authors integrated the component models with a published body composition model to develop a dynamic systems model of ME utilization that can accurately predict gain in empty BW resulting from the intake of a known amount of ME. The objective in this study is to test and evaluate the component models and the dynamic systems model of ME utilization.

Materials and Methods

Table 1 contains a list of acronyms used in this paper.

Overview

Williams and Jenkins (2003a) proposed a system of partitioning MEI, and Williams and Jenkins (2003a,b)

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Table 1. Glossary of terms

FBW	BW of animal that includes contents of the gastrointestinal tract, kg
EBW	FBW less weight of contents of gastrointestinal tract, kg
SREBW	EBW of mature cattle that contains 25% ether-extractable lipid, kg
dEBW	Change in EBW, kg/d
dFAT	Change in weight of ether-extractable lipid in EBW, kg/d
dFFM	Change in weight of ether-extractable lipid free mass in EBW, kg/d
dPRO	Change in weight of protein in EBW, kg/d
MEI	ME intake, Mcal/d
ME_m	ME used for maintenance, Mcal/d
H_iE_v	ME used for support metabolism, Mcal/d
ME_g	ME used for gain, Mcal/d
RE	Recovered energy, Mcal/d
RE_p	Recovered energy as protein, Mcal/d
k_p	Net partial efficiency of ME utilization for protein gain
k_f	Net partial efficiency of ME utilization for fat gain
k_g	Net efficiency of ME utilization for gain
kH_iE_v	ME requirement for support metabolism, kcal/kg FBW per multiple of ME_m intake above the ME_m requirement
kME_m	ME requirement for maintenance, kcal/kg of FBW

developed component models to predict daily changes in empty BW **(dEBW)** using MEI as the input. In these models, methods were developed to predict daily ME requirements for maintenance **(ME_m),** heat production associated with support metabolism **(H_iE_v),** ME available for gain **(ME_g),** net efficiency of ME utilization for gain **(k_g),** recovered energy **(RE)** from ME_g, and dEBW from RE. In this study, we will test the response of these component models within the integrated model and the response of the integrated model using experimental data to evaluate the predicted results. In these evaluations, the model of Williams et al. (1992) was used to convert empty BW (**EBW**) to full BW **(FBW).** All available experimental data on ME_m, as defined in the model by Williams and Jenkins (2003a), were used in model development; hence, further experimentation is needed to evaluate the ME_m model. In addition, it would also be very difficult to evaluate H_iE_v; therefore, the model to predict ME_g from MEI would not be evaluated. However, once other components of the integrated model have been successfully evaluated, then the evaluation of the integrated model would be an indirect evaluation of the model to predict ME_m and H_iE_v.

The model to predict RE from ME_g is based on estimating the net efficiency of ME utilization for gain **(k_g)** using net partial efficiencies of ME utilization for protein **(k_p)** and fat gain **(k_f)**; therefore, the estimates used for these net partial efficiencies will be evaluated. Several experiments have looked at the relationship between RE and MEI, and this relationship represents the marginal efficiency of ME utilization for gain when two different feeding levels are compared. When the integrated model is run to predict dEBW from MEI, simulated data on RE will be generated, and the predicted relationship between RE and MEI will be evaluated with observed data. Experimental data from the U.S Meat Animal Research Center **(MARC)** will be used to evaluate the model that predicts dEBW with RE as the input, and the entire model to predict dEBW

using MEI as the input. In summary, the following four areas will be evaluated: 1) net efficiency of ME utilization for gain, 2) relationship between RE and MEI, 3) predicting dEBW from RE, and 4) predicting dEBW from MEI.

Net Efficiency of Metabolizable Energy Utilization for Gain

Williams and Jenkins (2003b) used the following equation to predict k_g:

$$k_g = 0.75/(1 + 2.75 \times RE_p/RE)$$

where RE_p is energy recovered in protein. This equation resulted from the work of Geay (1984), who estimated net partial efficiencies of ME utilization for protein and fat gain of 0.2 and 0.75, respectively. This equation was evaluated with data from Blaxter and Wainman (1961), based on three sheep and three steers that were fed the same feed at two levels below and three levels above maintenance.

The values 0.2 and 0.75 for k_p and k_f, respectively, were evaluated with data on 65 treatment means from 216 heifers and 208 steers, published by Lofgreen and Garrett (1968). Observed means in these data were for EBW, dEBW, MEI, and RE, and energy values were in kcal/kg of $EBW^{0.75}$. The observed means for dEBW and RE were used to calculate mean values for dPRO and dFAT as shown in the following equations:

$$RE = dPRO \times 5.7 + dFAT \times 9.5$$

$$RE = dFFM \times 0.243 \times 5.7 + dFAT \times 9.5$$

$$RE = (dEBW - dFAT) \times 1.39 + dFAT \times 9.5$$

$$RE = 1.39 \times dEBW + 8.11 \times dFAT$$

where 0.243 (Williams et al., 1995b) was used to represent the average fraction of protein in dFFM, and 5.7 and 9.5 represent the amount of energy in Mcal/kg of DM of protein and fat, respectively (Brouwer, 1965). The only unknown in this equation is dFAT, and we can predict it as a function of RE and dEBW with the following equation:

$$dFAT = (RE - 1.39 \times dEBW)/8.11$$

and calculate dPRO as follows:

$$dPRO = (dEBW - dFAT) \times 0.243$$

The observed mean value for MEI and calculated mean values for dPRO and dFAT were used in multiple regression analysis to partition MEI to protein and fat deposition as shown in the following equation:

$$MEI = b_0 + b_1 \times dPRO + b_2 \times dFAT$$

The intercept (**b_0**) in this equation is interpreted as an estimate of the maintenance requirement (kcal/kg of $EBW^{0.75}$), and the partial regression coefficients b_1 and b_2 represent the amounts of ME required for the deposition of 1 kg of protein and fat, respectively. The coefficients obtained in this regression analysis were used to calculate values for k_p and k_f as $5.7/b_1$ and $9.5/b_2$, respectively.

The Relationship Between RE and MEI

The marginal efficiency is the ratio of an increment in RE to the increment in energy intake when two feeding levels are compared. In growing and fattening ruminants, Blaxter and Graham (1955) and Blaxter and Boyne (1978) observed a curvilinear relationship between RE and GE intake throughout a range of food intake from zero to maximal. In these data, constant increments in daily GE intake resulted in progressively smaller increments in daily RE. Emmans and Kyriazakis (1995) analyzed the sheep data from Blaxter and Wainman (1961) and Graham (1969a) on RE and MEI and found no evidence that a continuously decreasing marginal efficiency described the data better than a constant marginal efficiency. Data from Blaxter et al. (1966) on RE and MEI both expressed in terms of kcal/kg of $BW^{0.73}$ showed no evidence for a decreasing marginal efficiency as MEI increased.

The main explanation for a continuously decreasing marginal efficiency is that as intake level increases, rate of passage and fecal losses of energy increase, resulting in decreased diet digestibility; hence, it is assumed that metabolizability of the diet would also decrease. It has been shown that as level of intake increases in both cattle and sheep, there is a decline in the proportional losses of methane and energy in urine (Blaxter and Clapperton, 1965; Blaxter et al., 1966; Flatt et al., 1969). The net result is that upon raising the intake level, the increase in the proportional fecal loss of energy tends to be balanced by a decrease in the proportional losses of methane and energy in the urine, and metabolizability of the gross energy is less affected than digestibility. Results of analyses of 80 sets of experimental data on cattle and sheep by Blaxter and Boyne (1978) support a constant metabolizability of GE with increasing feeding level. This result was also obtained by Wurgler and Bickel (1987) with three breeds of cattle fed at two levels of intake. These authors found small increases in metabolizability with increased feeding level, but this result was probably not significant.

The metabolic processes that predominate at negative and positive energy retention are quantitatively and qualitatively different (Armstrong and Blaxter, 1957a,b), and Blaxter and Wainman (1961) suggested that food utilization for maintenance is dealt with separately from food utilization above maintenance. Blaxter and Wainman (1961) and ARC (1980) proposed that food intake be expressed in terms of ME to account for any affects of increasing food intake on digestibility, and suggested that no great error was involved if the continuous curvilinear relationship between daily rate of energy retention and rate of food intake expressed as ME was approximated by two straight lines, one applying from fasting to zero energy retention and the other for positive energy retention. This linear relationship between RE and MEI above zero energy retention was obtained by Blaxter et al. (1966) in cattle aged 15 to 81 wk, and the marginal efficiency in these data was 0.557.

Williams and Jenkins (2003a) showed that using a model such as that proposed by Turner and Taylor (1983) in which incremental heat production above MEI at zero energy balance is treated as a single dynamic pool, RE would be represented by the following equation:

$$RE = k_g \times (MEI - ME_m)$$

The marginal efficiency is the first derivative of RE with respect to MEI, which is k_g, and since $MEI - ME_m$ is ME_g, the net efficiency which is the first derivative of RE with respect to ME_g is also k_g. Thus, with this system of partitioning, net efficiency and marginal efficiency are the same. In the system of partitioning MEI proposed by Williams and Jenkins (2003a), the following expression was developed for RE:

$$RE = k_g \times (MEI - ME_m - H_iE_v) \qquad [1]$$

In this system, $MEI - ME_m - H_iE_v$ is ME_g; hence, net efficiency is still k_g, but marginal efficiency is different because H_iE_v is a function of MEI.

The dynamic model of ME utilization developed by Williams and Jenkins (2003a,b) was formulated on biological principles of ME utilization for maintenance, support metabolism, and production without any considerations about the marginal efficiency of ME utiliza-

tion for gain. The expression for RE in Eq. [1] will be used to show how marginal efficiency is calculated in this model. First, the term H_iE_v is replaced by the right hand side of Eq. [11] of Williams and Jenkins (2002a) and MEI/ME_m is used to represent level of feeding (MM):

$$RE = k_g \times [MEI - ME_m - kH_iE_v \times (MEI/ME_m - 1) \times FBW]$$

Replacing the second ME_m term by $kME_m \times FBW$ and multiplying by FBW we derive

$$RE = k_g \times [MEI - ME_m - kH_iE_v \times (MEI/kME_m - FBW)]$$

$$RE = k_g \times [MEI - ME_m - (kH_iE_v/kME_m) \times (MEI - ME_m)]$$

$$RE = k_g \times (MEI - ME_m) \times (1 - kH_iE_v/kME_m) \quad [2]$$

The terms kH_iE_v and kME_m are breed parameters and estimates for 21 purebreds evaluated at MARC were published by Williams and Jenkins (2003a). Hence, the term $(1 - kH_iE_v/kME_m)$ is a breed constant and Eq. [2] can be written as follows:

$$RE = C \times k_g \times (MEI - ME_m) \quad [3]$$

where C is $1 - kH_iE_v/kME_m$.

For Hereford × Angus cattle, estimates of kH_iE_v and kME_m are 8.7 and 27.8 kcal, respectively, with a diet containing 2.84 Mcal of ME/kg of DM; therefore, the value of C would be 0.69. In this case, 69% of MEI above ME_m would be partitioned to ME_g and 31% to H_iE_v. The derivative of RE, with respect to MEI, in Eq. [3] is C × k_g, which means that MEI above ME_m is retained at the rate C × k_g. This solution for marginal efficiency defines the relationship between RE and MEI above ME_m in the model, and depending on the value of k_g, this relationship may be linear or curvilinear. In experiments where animals of approximately the same weight are fed different amounts of the same diet, there may be little differences in k_g, which would result in a constant marginal efficiency.

Experimental data from Blaxter and Graham (1955), Blaxter and Wainman (1961), Lofgreen and Garrett (1968), and Graham (1969a,b) were used to investigate the relationship between RE and MEI. Data above zero RE were selected and grouped into subsets based on experiment, species (sheep, cattle), breed, and sex. Within experiment, heat production was regressed on RE and the intercept of the resulting regression, which is an estimate of the MEI at zero energy retention, was used to scale RE and MEI within each experiment. Scaled RE was then regressed on linear and quadratic terms for scaled MEI in data subsets and in the total cattle and sheep data, respectively.

The model was used to investigate the relationship between predicted response in RE and observed MEI by simulating the growth and body composition of Hereford × Angus steers during the finishing phase in the first three cycles of the Germplasm Evaluation (**GPE**) project at MARC, under two scenarios. In the first scenario, growth and body composition of steers were simulated from weaning to slaughter to match the observed data, and simulated results were used to evaluate the relationship between RE and MEI over the finishing period. In the second scenario, similar nutritional treatments as the sheep experiment of Graham (1969a) were used since very high levels of ME were consumed in this study. In this scenario, Hereford × Angus steers were grown up to 400 kg of FBW with an MEI of 1.5 times their ME_m. Steers were then fed for 20 d at nine levels of MEI ranging from 0.5 to 4.5 times their ME_m in increments of 0.5, and simulated data on the average RE over the 20 d were used to investigate the response in marginal efficiency over the range of feeding levels.

Prediction of dEBW from RE

The component model to predict dEBW using RE as the input was evaluated against data from Ferrell and Jenkins (1998), collected from steers sired by Angus, Boran, Brahman, Hereford, or Tuli bulls, out of MARC III (¼ Angus, Hereford, Pinzgauer, and Red Poll) dams. Weaned steers were either limit fed or had ad libitum access to a high concentrate diet and were slaughtered after approximately 140 d on feed. Average values of RE over the feeding period were predicted from the chemical composition of initial and final slaughter groups, within sire breed and energy intake subclass. The accuracy of the component model to predict dEBW from RE was evaluated in terms of its ability to predict the mean slaughter EBW of steers within sire breed and energy intake subclass using RE as the input. Estimates of breed parameters for these steers were obtained from Williams et al. (1995a). For Brahman-sired steers, parameters for crossbred Brahman steers were used. For Boran- and Tuli-sired steers, parameters for Sahiwal crossbred steers were used, and parameters for Hereford-sired steers were used for Hereford- and Angus-sired steers because of the similarity in growth and composition of these steers. Values for SREBW were all increased by 20% to account for the larger size of MARC III dams, compared with the average of Angus and Hereford dams in the first three cycles of the GPE project.

Prediction of dEBW from MEI

The ability of the integrated model to predict observed responses in dEBW using MEI as the input will depend on how accurately the component models predict the outputs of the subsystems they represent and also how well these component models interact with each other to predict the overall observed results. In

this case, evaluation of the integrated model will also be an indirect evaluation of the component models used to predict ME_m and H_iE_v. The ability of the model to predict dEBW using MEI as the input was evaluated by simulating growth of four breeds of steers over the finishing period and FBW changes in three breeds of reproducing females from 10 mo to 7 yr of age.

Steers were purebred Hereford and Angus, crossbred Jersey, and Charolais in the GPE project, and purebred Charolais on low and high planes of nutrition in the Germplasm Utilization **(GPU)** project at MARC. For each type of steer in the GPE project and each feeding level in the GPU project, MEI was obtained with equations that were derived from feed intake data, and this was used as the input to the model. The average ME density of the diet in the first three cycles of the GPE project and the low level of feeding in the GPU project was approximately 2.84 Mcal/kg of DM and breed values for kME_m and kH_iE_v estimated at this dietary ME density (Williams and Jenkins, 2003a) were used. The ME density of the diet used for the high level of feeding in the GPU project was 3.07 Mcal/kg of DM, and kME_m and kH_iE_v values for Charolais steers on this feeding level were adjusted for ME density of the diet using equations for the efficiency of ME utilization for maintenance from NRC (2000).

Reproducing females were Angus, Charolais, and Simmental cows at MARC. Nutritional and FBW data were recorded on these females over their life cycle. The Angus represented moderate growth and mature size, moderate milk production, and easy fattening; Charolais represented high growth and large mature size, moderate milk production, and poor fattening; and Simmental represented high growth and large mature size, high milk production, and poor fattening. Measurements of FBW of individual females were recorded at brand clipping, at the start of the breeding season, and at palpation each year, starting at 10 mo of age and continuing up to 7 yr of age. Nutritional data over the same period were used to calculate daily MEI. Growth and body composition of the females were predicted on a daily basis using MEI as input, and predicted data on FBW changes were compared with the observed data.

Results and Discussion

Net Efficiency of ME Utilization for Gain

Results from Blaxter and Wainman (1961) showed that the net efficiency of ME utilization for gain calculated from the regression of RE on MEI above maintenance was 0.535 and 0.514 for the sheep and steers, respectively. The energy recovered as protein was 14.6 and 15.5% of total energy recovered by the sheep and steers, respectively. Using Eq. [2] from Williams and Jenkins (2003b), with RE_p/RE values of 0.146 and 0.155, the calculated k_g values for the sheep and steers were 0.535 and 0.526, respectively. These predicted val-

ues for the net efficiency of ME utilization for gain were not much different from the observed values, which support values of 0.2 and 0.75 for the partial net efficiencies of ME utilization for protein and fat gain, respectively.

The results of the linear regression of MEI on dPRO and dFAT obtained from data on 65 treatment means published by Lofgreen and Garrett (1968) were as follows:

$$MEI = 0.12 + 31.95 \times dPRO + 15.41 \times dFAT$$
$$(R^2 = 0.87, SE = 0.024)$$

The resulting estimates of k_p and k_f are 5.7/31.95 = 0.18 and 9.5/15.41 = 0.62. These estimates are probably underestimated because the model may be partitioning too little ME to maintenance and support metabolism (0.12 Mcal/kg of $EBW^{0.75}$) for animals with a high MEI. In this case, ME_g would be overestimated, resulting in lower values for k_p and k_f. Studies in which maintenance ME requirements were obtained at different levels of feeding showed that these requirements increased by 13.6% (Birkelo et al., 1991; cattle), 15 to 18% (Gray and McCracken, 1979; pigs), and 15% (Thorbek and Henkel, 1976; cattle) per multiple of the ME equivalent of FHP intake. These results support about a 15% increase in maintenance ME requirements per multiple of the ME equivalent of the fasting heat production intake, and this was used to estimate the cost of support metabolism in the data and reanalyze the data after adjusting for support metabolism.

The estimate of maintenance requirement in the above analysis was used to calculate the multiple of maintenance intake for each treatment mean as MEI/0.12, and support metabolism was calculated as 15% of the maintenance requirement for each multiple of intake above 0.12 Mcal/kg of $EBW^{0.75}$. The estimate of support metabolism and maintenance requirement was then subtracted from MEI and the remaining MEI was regressed on dPRO and dFAT. The results of this analysis were as follows:

$$MEI = 0.0 + 27.16 \times dPRO + 13.1 \times dFAT$$
$$(R^2 = 0.87, SE = 0.02)$$

These results show that the intercept was not significantly different from zero; hence, we have completely accounted for the maintenance requirement plus support metabolism, and the remainder of the MEI is now partitioned between protein and fat. The efficiencies of protein and fat deposition in this analysis are 5.7/27.16 = 0.21 and 9.5/13.1 = 0.73, respectively, and these efficiencies are similar to the mean efficiencies of 0.2 and 0.75 used that were used by Williams and Jenkins (2003b).

Relationship Between RE and MEI

Results of regressions using experimental data of RE and MEI, both divided by MEI at zero RE, are shown in Table 2. Two additional regressions were done, one

Table 2. Coefficients with standard errors in parentheses, coefficients of determination, and standard errors, from regressions of scaled RE on linear, and linear and quadratic terms for scaled MEI[a,b]

Source	Animals	n	$f(x) = b_0 + b_1 x$			$f(x) = b_0 + b_1 x + b_2 x^2$			
			b_1	R^2	SE	b_1	b_2	R^2	SE
Blaxter and Graham (1955)	Two sheep	9	0.472 (0.034)	0.96	0.052	0.289 (0.273)	0.048 (0.071)	0.97	0.054
Blaxter and Wainman (1961)	Three sheep	12	0.524 (0.038)	0.95	0.072	0.714 (0.335)	−0.046 (0.081)	0.95	0.074
	Three steers	9	0.474 (0.066)	0.88	0.063	0.851 (0.695)	−0.108 (0.199)	0.89	0.067
Graham (1969a)	Four sheep	5	0.485 (0.013)	0.99	0.031	0.563 (0.069)	−0.015 (0.013)	0.99	0.029
Graham (1969b)	Eight sheep	6	0.511 (0.019)	0.99	0.047	0.663 (0.099)	−0.031 (0.019)	0.99	0.041
Lofgreen and Garrett (1968)[c]	Cattle	25	0.391 (0.029)	0.87	0.079	0.139 (0.234)	0.071 (0.065)	0.89	0.078
	Cattle	34	0.437 (0.014)	0.97	0.041	0.368 (0.180)	0.018 (0.046)	0.97	0.041
All sheep data	—	—	0.502 (0.016)	0.97	0.071	0.603 (0.079)	−0.021 (0.016)	0.97	0.071
All cattle data	—	—	0.421 (0.016)	0.91	0.068	0.405 (0.154)	0.005 (0.042)	0.91	0.069

[a]In all experimental data, RE and MEI were divided by the MEI at zero energy retention. For abbreviation definitions, see Table 1.
[b]$f(x)$ = scaled RE, and x = scaled MEI.
[c]These data were means.

with all the sheep data and the other using all the cattle data. All regressions with the linear model showed a very strong relationship between RE and MEI, with the regression coefficient for MEI being highly significant. Regressions with the quadratic model also showed a similar strong relationship between RE and MEI; however, there was no evidence that the coefficient for MEI^2 in the quadratic model was significantly different from zero in all the regressions. In the linear model, the regression coefficient b_1 represents the marginal efficiency. The average marginal efficiencies for the sheep and cattle data were 0.502 and 0.421, respectively. The sheep data were collected over 2 d at specific points in time, whereas the majority of the cattle data (Lofgreen and Garrett, 1968) were average data over a long feeding period.

The average marginal efficiencies for the sheep and cattle data support the concept of a metabolic lag in heat production attributable to support metabolism when animals are switched from one plane of nutrition to another. In the sheep data, the distributed lag function used in Eq. [13] of Williams and Jenkins (2003a) for $H_i E_v$ would result in very little change in $H_i E_v$ as level of feeding level increased, and according to Eq. [1], if ME_m is assumed to be constant, then increases in MEI would be recovered at a rate that is close to k_g. In the cattle data, the impact of previous plane of nutrition on $H_i E_v$ would have been minimal due to the long feeding period and, in this case, the marginal efficiency would be closer to $C \times k_g$, as shown in Eq. [3]. These results would also explain why efficiencies of ME utilization obtained in comparative slaughter trials are smaller than those obtained for similar feeds by calorimetric measurements of energy balance.

Predicted results for ME_g and RE, both expressed as multiples of ME_m, obtained from simulating growth and body composition of Hereford × Angus steers, are plotted in Figure 1 against input values for MEI expressed as a multiples of ME_m. Input values for scaled MEI decreased from 3.28 at the start to 2.07 at the end of the finishing period; thus, relationships will be dis-

cussed from right to left along the x-axis. Scaled ME_g was highest at the start of the finishing period and decreased at a decreasing rate up to about two-thirds of the finishing period, after which the rate of decrease was almost constant. This response was due to the fact that steers were put on a conditioning diet before the start of finishing, and cost of support metabolism was low. This low cost was lagged into the finishing period, which caused ME_g to be high at the start and decrease at a decreasing rate over the initial part of the finishing period.

To evaluate the slope of the ME_g curve with respect to MEI, the following equation for ME_g was derived from Eq. [3] by dividing both sides by k_g, and then replacing RE/k_g by ME_g:

$$ME_g = C \times (MEI − ME_m)$$
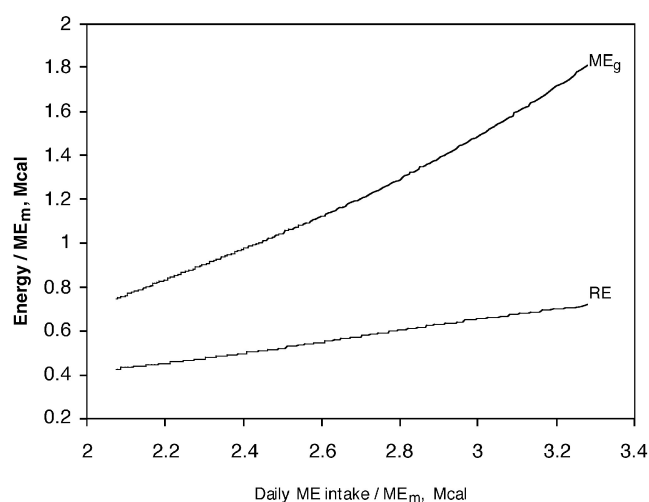
Figure 1. Predicted results for ME_g and RE, both expressed as multiples of ME_m, obtained from simulating growth and body composition of Hereford × Angus steers, averaged over the first three cycles of the Germ-plasm Evaluation Project.

The first derivative of ME_g, with respect to MEI, in this equation is C; therefore, the slope of the ME_g line in Figure 1 should gradually approach the value of C as days on feed increases. The value of C for Hereford × Angus steers on a diet containing 2.84 Mcal of ME/kg of DM is 0.69, and the slopes of the ME_g curve in Figure 1, at scaled MEI values of 2.6 and 2.2 to the end of the finishing period, were 0.72 and 0.69, respectively.

The relationship between RE and MEI was similar, but at the start of the finishing period, scaled RE decreased at an increasing rate up to a scaled MEI value of about 2.6, after which the rate of decrease was almost constant. This response is due to the effects of the previous nutritional treatment on daily gain. Daily gain was low prior to the start of the finishing period, and this resulted in a greater fraction RE going to protein and a lower value for k_g. This low daily gain was lagged into the finishing period, which caused k_g to be lower than if previous daily gain was higher. As days on feed increased from the start of finishing, k_g increased at faster rate initially, and this more than compensated for the initial large decreases in ME_g, resulting in a slower initial decrease in RE.

The simulated results in Figure 1 cover the entire finishing period from weaning to slaughter. As MEI increased, FBW and ME_m also increased, and in this case ME_m would be a function of MEI, which would result in the first derivative of RE with respect to MEI in Eq. [3] being more complicated than $C \times k_g$. Therefore, we will look at the average response in RE to MEI. The average slope of RE was 0.208, which means that 20.8% of MEI was retained in the finishing period, and this compares with 20.3% for the average of Hereford × Angus steers over the first three cycles of the GPE project. The following expression for RE/MEI can be derived from Eq. [3] by dividing both sides by MEI:

$$RE/MEI = C \times k_g \times (MEI/MEI - ME_m/MEI)$$

In the simulated data, the value of k_g increased from 0.39 at the start to 0.57 at the end of the finishing period. The average value of k_g was 0.51, the average value of ME_m was 41% of MEI, and for Hereford × Angus steers, the value for C was 0.69. Therefore, the average value of RE/MEI would be $0.69 \times 0.51 \times (1 - 0.41) = 0.208$, which is the same as the slope of RE in Figure 1. The average marginal efficiency of Angus and Hereford steers on low and high planes of nutrition (Ferrell and Jenkins, 1998) was 21%, and this compares reasonably well with 20.8% for Hereford × Angus steers in the GPE project that had intermediate growth rates.

Data on feedlot closeouts for March and April 2001 (Hoelscher, 2001) were used to calculate the fraction of MEI that was recovered during the finishing period. Steers were placed on feed at 320 kg and finished at 530 kg, dry feed conversion was 6.82, feed was assumed to contain 3.2 Mcal of ME/kg of DM, and gain was assumed to contain 6.3 Mcal/kg. In these data, RE averaged 26.5% of MEI over the finishing period. This higher
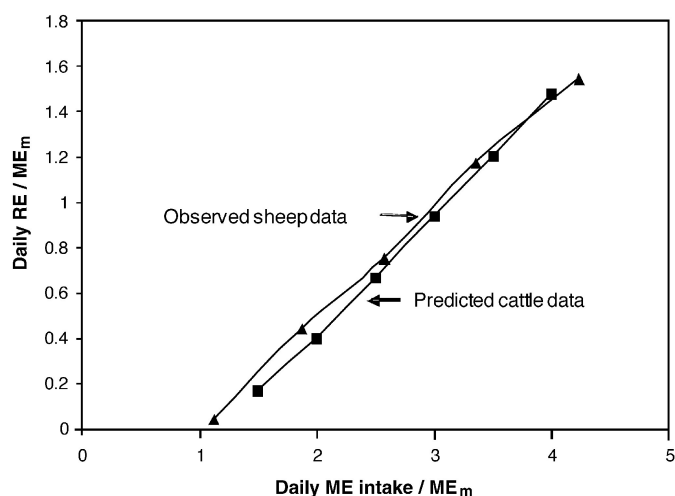
Figure 2. Observed results (Graham, 1969a) on RE response to MEI both scaled by ME intake at zero energy retention for four sheep that were fed at seven different levels including zero intake, and predicted results on RE response to MEI both scaled by ME_m for Hereford × Angus steers that were fed at levels ranging from 0.5 to four times their ME_m requirements.

efficiency, compared with the GPE data, is possibly a result of compensatory growth (steers were long yearlings when placed on feed), a higher quality finishing diet, and lower H_iE_v. The lower H_iE_v is a result of stocking, a shorter finishing period, and the distributed lag function used for H_iE_v.

Observed results for RE and MEI (Graham, 1969a), both scaled by MEI at zero energy retention, for four sheep that were fed at seven different levels, including zero intake, are shown in Figure 2, together with simulated results scaled by ME_m for Hereford × Angus steers fed at similar levels of MEI. Regression analysis showed a strong significant linear relationship between RE and MEI in the observed and predicted data, with very little evidence for curvilinearity. The slopes for the observed sheep and predicted cattle data were 0.485 and 0.525, and these slopes represent the marginal efficiencies. These marginal efficiencies are much greater than the $C \times k_g$ derived from Eq. [3], and this is mainly due to the fact that measurements were taken over a short feeding period. In this case, the distributed lag function used in Eq. [13] of Williams and Jenkins (2003a) for H_iE_v would result in very little change in H_iE_v as level of feeding level increased, and according to Eq. [1], if ME_m is assumed to be constant, then increases in MEI would be recovered at a rate that is close to k_g.

Prediction of dEBW from RE

Simulated results for the experiment of Ferrell and Jenkins (1998) are shown in Figure 3, where observed values for final EBW are plotted against predicted values. Pairs of values (observed and predicted) tend to lie
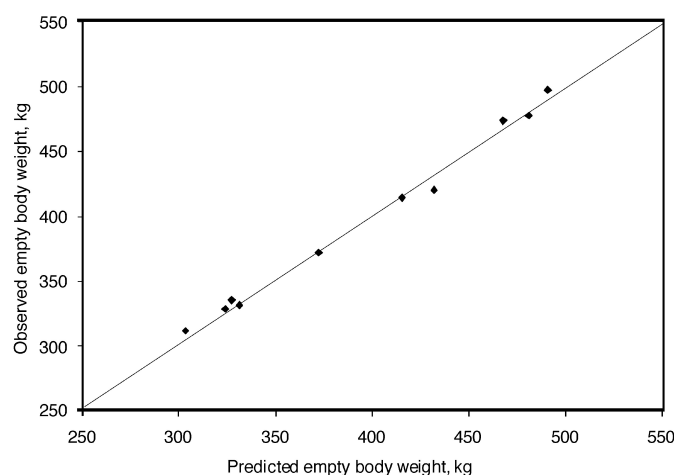
Figure 3. Observed values for final EBW of steers sired by Angus, Boran, Brahman, Hereford, or Tuli bulls out of MARC III (¼ Angus, Hereford, Pinzgauer, and Red Poll) dams, plotted against predicted values for EBW. Observed data from Ferrell and Jenkins (1998).

close to the 45° line, and this is evidence that the model can predict the actual system. Linear regression of observed on predicted values for EBW resulted in an intercept and slope that were not significantly different ($P < 0.05$) from 0 and 1, respectively. These results were interpreted to suggest that the model could accurately predict the actual system.

Prediction of dEBW from MEI

Results obtained from using MEI as input to simulate the growth of Hereford, Angus, crossbred Jersey, and Charolais steers in the GPE project, and purebred Charolais steers on low and high planes of nutrition in the GPU project at MARC, are shown in Table 3. Except for Charolais steers on the high diet (3.07 Mcal of ME/

Table 3. Observed and predicted final EBW for different biological types of steers in the Germplasm Evaluation (GPE) and Germplasm Utilization (GPU) Projects at MARC

	Final EBW, kg	
Biological type[a]	Observed	Predicted
GPE Project		
Hereford	408	405
Angus	415	409
Jersey ×	395	394
Charolais ×	457	464
GPU Project[b]		
Charolais (low)	491	484
Charolais (high)	521	522

[a]Jersey × = ½ (Jersey × Angus + Jersey × Hereford), etc. For abbreviation definitions, see Table 1.
[b]ME densities of the low diet and high diet were 2.84 and 3.07 Mcal/kg of DM, respectively.
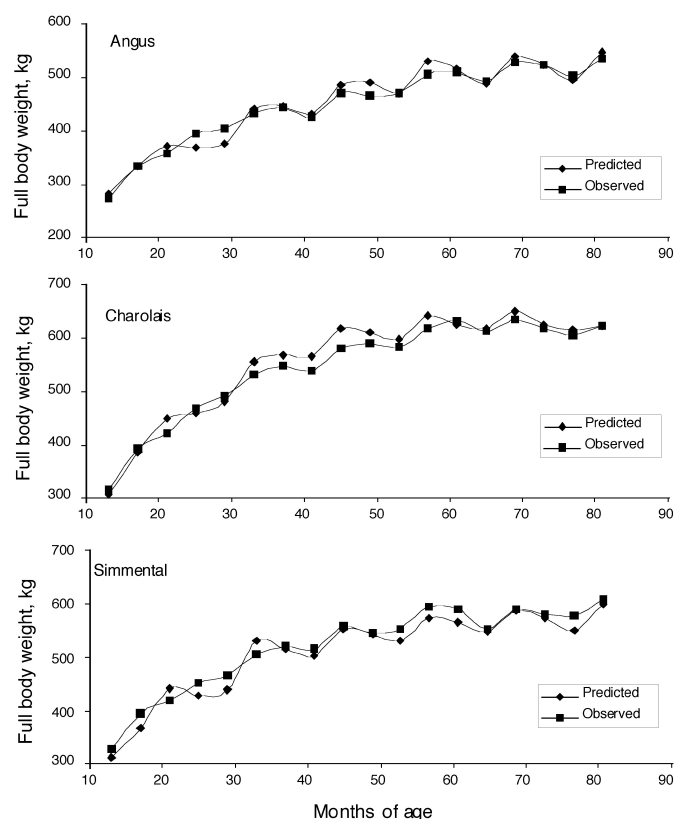
Figure 4. Observed and predicted FBW for Angus, Charolais, and Simmental females at MARC from 10 mo to 7 yr of age.

kg of DM), the average ME density of the diet in these experiments was 2.84 Mcal of ME/kg of DM, and breed values for kME_m and kH_iE_v published by Williams and Jenkins (2002a) were used. Efficiencies of ME utilization for maintenance calculated according to NRC (2000) for the diets containing 2.84 and 3.07 Mcal of ME/kg of DM were 0.67 and 0.68, respectively. Breed values for kME_m and kH_iE_v for Charolais steers on the high diet were multiplied by the ratio 0.67/0.68 to adjust for the higher quality diet. The adjusted values for kME_m and kH_iE_v were 27.31 and 8.35 kcal, respectively. Linear regression of observed on predicted values for EBW resulted in an intercept and slope that were not significantly different ($P < 0.05$) from 0 and 1, respectively. These results were interpreted to suggest that the integrated model could accurately predict the actual system.

Predicted results for changes in FBW from 10 mo to 7 yr of age for Angus, Charolais, and Simmental reproducing females at MARC are shown in Figure 4. The model tended to overpredict FBW for Angus and Charolais, and underpredict FBW for Simmental females between 40 to 60 mo of age. These results may be due to errors in estimating MEI; however, the model was able to predict the growth pattern of the three breeds over the 7-yr period using MEI. One important result is that there was a close agreement between

predicted and observed FBW between 60 to 84 mo of age. This is evidence that the component models used to predict ME_m and H_iE_v were accurate since errors in predicting these two components of heat production would accumulate and result in large over- or underpredictions in FBW over time.

Implications

Component models of an integrated system model to predict daily body weight gain using metabolizable energy intake as the input were shown to provide accurate predictions of observed responses of the represented sub-systems, and evaluations of the integrated system showed that it provided an accurate representation of the real system. The effect of previous and present level of feeding on requirements for metabolizable energy is modeled as a distributed lag function of support metabolism, which increased the prediction accuracy of the model under varying levels of nutritional management. The integrated system model is used as a complete package in decision support software to assist beef producers in evaluating the impact of strategic management decisions on future productivity. The maintenance, support metabolism, and efficiency of metabolizable utilization for gain components may be used with a different set of assumptions to develop other system models.

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